Comparative Chewing Efficiency in Mammalian Herbivores

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Comparative chewing efficiency in mammalian herbivores

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Although the relevance of particle size reduction in herbivore digestion is widely appreciated, few studies have investigated digesta particle size across species in relation to body mass or digestive strategy. We investigated faecal particle size, which reflects the size of ingesta particles after both mastication and specialized processes such as rumination. Particle size was measured by wet sieving samples from more than 700 captive individuals representing 193 mammalian species. Using phylogenetic generalized least squares, faecal particle size scaled to body mass with an exponent of 0.22 (95% confidence interval: 0.16–0.28). In comparisons among different digestive strategies, we found that (1) equids had smaller faecal particles than other hindgut fermenters, (2) non-ruminant foregut fermenters and hindgut fermenters had similar-sized faecal particles (not significantly different), and (3) ruminants had finer faecal particles than non-ruminants. These results confirm that the relationship between chewing efficiency and body mass is modified by morphological adaptations in dental design and physiological adaptations to chewing, such as rumination. This allometric relationship should be considered when investigating the effect of body size on digestive physiology, and digestion studies should include a measure of faecal particle size.

Mammals are the 'definite chewers' (Reilly et al. 2001). They have evolved remarkable variations in dental design, a high degree of convergent dental adaptations, and physiological adaptations that involve regurgitating the contents of a proximal gastrointestinal compartment and re-masticating them (i.e. rumination). The latter mechanism is characteristic of ruminants and camelids, where a certain fraction of the forestomach contents is regurgitated. In several other animals, such as some macropods and koalas *Phascolarctos cinereus* (Hume 1999) and possibly the capybara *Hydrochorus hydrochaeris* (Lord 1994), food from the simple stomach is sometimes regurgitated and re-masticated; this process is called 'merycism', but it is not observed with the same consistency as rumination. Relationships between tooth design, chewing physiology and diet properties have been assumed since antiquity (summarized in Evans et al. 2007). However, comparative tests of chewing efficiency are rare.

The relevance of reducing the particle size of ingested food is well understood, particularly in herbivores (Clauss and Hummel 2005). Specifically, smaller food particles can be digested at a much faster rate. Particle size reduction – either by dental mastication (mammals) or by grinding in a gastric mill (birds) – is often considered the key digestive difference between ecto- and endotherms. Although both ecto- and endotherms achieve similar degrees of digestive efficiency per unit of ingested food, endotherms do so at a faster rate, thus allowing for the higher food intake rate necessary to fuel endothermy (Karasov et al. 1986). Within mammals, a tradeoff between ingesta retention time and ingesta particle size has been suggested. In focused comparisons of small groups of species, variation in chewing efficiency has been invoked to explain observations of digestive efficiency that could not be explained by differences in ingesta retention (e.g. among the horse, rhinoceros and elephant (Clauss et al. 2005), the buffalo and hippopotamus (Schwarm et al. 2009), and within the sexually dimorphic ibex (Gross et al. 1996)). Within species, differences in dental efficiency (e.g. due to wear) may be compensated for by different food intake rates and/or differences in chewing times (Pérez-Barberìa and Gordon 1998b, Logan 2003).

A convenient way to assess chewing efficiency is to measure faecal particle size. This measure is independent of further digestive processes, with several studies demonstrating that bacterial fermentation (digestion) has little influence on particle size reduction in the digestive tract of terrestrial mammalian herbivores (Poppi et al. 1980, Murphy and Nicoletti 1984, McLeod and Minson 1988a, Spalinger and Robbins 1992). Similarly, no further reduction in digesta particle size occurs beyond the forestomach from which digesta is regurgitated in the ruminant (and camelid) digestive tract. This finding indicates that other digestive processes (acid and enzymatic digestion in the abomasum and small intestine; bacterial fermentation in the hindgut) have little effect on particle size (Poppi et al. 1980,

Udén and Van Soest 1982, McLeod and Minson 1988b, Lechner-Doll and von Engelhardt 1989, Freudenberger 1992). Fewer studies have been published for non-ruminants, probably because an investigation of digesta particle size along a non-ruminant's digestive tract is unlikely to reveal differences between different sections. However, existing data for non-ruminant foregut fermenters – macropods (Freudenberger 1992) and sloths (Foley et al. 1995) – indicate little change in ingesta particle size from the forestomach to the faeces.

One of the most cited advantages of an increase in body mass (BM) in herbivores is a presumed increase in efficiency of digestion. As gut capacity increases with $BM^{1.00}$, but energy requirements, and hence food intake, increase with $BM^{0.75}$, larger animals should have more gut capacity available per unit ingested food, which produces an expected allometric scaling exponent of $BM^{0.25}$ for ingesta retention time (Parra 1978, Demment and Van Soest 1985, Illius and Gordon 1992, but see Clauss et al. 2007). This suggests that larger animals should experience advantages in terms of digestion.

Yet, larger animals might also experience digestive disadvantages (Clauss and Hummel 2005), including an increase in ingesta particle size (Pérez-Barberìa and Gordon 1998a). Apart from everyday observations (e.g. on faeces of rabbits and horses), a few studies on limited numbers of species indicate that faecal particle size increases with body mass (Udén and Van Soest 1982, Clauss et al. 2002). The intuitive reason for this is that in the larger teeth of larger mammals, structures responsible for particle size reduction, such as distances between enamel ridges, are of a coarser scale than in smaller animals. In addition to variation in body mass, some mammals possess digestive strategies that enable them to process food more efficiently. These include, for example, dental adaptations in equids, and rumination in other ungulates, which could cause deviations from the underlying allometry of faecal particle size.

Although an allometric relationship between ingesta particle size and body mass has been suspected (Pérez-Barberìa and Gordon 1998a), body size considerations have received less attention in the comparative analysis of ingesta particles. Here, we investigated the scaling of ingesta particle size across a dataset of 193 mammalian species. We also performed three nested comparisons in the dataset to further illuminate factors that influence ingesta particle size. First, across the entire dataset, we investigated whether ruminants achieve a smaller ingesta particle size than non-ruminants of similar body size. This is an important test because ruminants are thought to possess more efficient digestive capabilities, in part through their method of reducing ingesta particle size by rumination. Second, among the non-ruminants, we investigated whether ingesta particle size differs between foregut and hindgut fermenters. This comparison is important because non-ruminant foregut fermentation has often been equated with ruminant foregut fermentation (Moir 1965, Janis 1976), whereas some comparisons indicate that these groups could be very different in terms of chewing efficiency, with ruminants consistently producing finer particles (Langer 1988, Freudenberger 1992, Clauss et al. 2004, Schwarm et al. 2009). Lastly, among the hindgut fermenters, we tested whether equids generate smaller particles, which we proposed would occur due to their particularly efficient dental design (Rensberger 1973, Jernvall et al. 1996). Throughout, we used both phylogenetic and non-phylogenetic methods to investigate the comparative patterns.

Methods

Faecal samples were collected from captive individuals of 193 mammalian species (including previously published data from Clauss et al. 2002), with 1–18 samples per species, depending on the access to individuals (Appendix 1). Samples originated from apparently healthy, adult animals without a history of dental or digestive disease who were offered a diet that also included a relevant source of fibre. Body mass was either known for the individuals sampled, estimated, or taken from the literature. Especially in the case of small animals, we often had to use group samples, pooling faeces from different individuals (marked as gs in the Appendix 1), to attain the amounts required for analysis. Faeces were analysed by wet sieving. Mean faecal particle size calculated by wet sieving over a series of sieves with mesh sizes of 4, 2, 1, 0.5, 0.25 and 0.125 mm, and subsequent calculation of the mean particle size after fitting a suitable function to the respective sample data using TableCurve 2D v5.01 (Systat Software; Hummel et al. 2008). For each species, an average mean particle size was calculated that was used in the subsequent analyses. Species were classified as hindgut fermenters (i.e. colon or caecum fermenters), non-ruminant foregut fermenters and ruminants (including the Ruminantia and the Tylopoda).

We investigated the scaling of faecal particle size using both non-phylogenetic tests and phylogenetic generalized least squares (PGLS). PGLS provides an approach to studying correlated evolution (Martins and Hansen 1997, Garland and Ives 2000), and becomes increasingly attractive for comparative biologists due to its flexibility. For phylogenetic tests, we based our analyses on the phylogeny from Bininda-Emonds et al. (2007). Calculation of PGLS was conducted using BayesTraits (Pagel and Meade 2007). Codes reflecting digestion type (ruminants, non-ruminants, non-ruminant foregut fermenters, hindgut fermenters) or taxonomic group (equids) were included as a dummy variable in the regression model. We also investigated whether body mass and faecal particle size showed phylogenetic signal, i.e. whether more closely related species exhibit similar trait values, as calculated in BayesTraits (Pagel and Meade 2007). For this, we calculated the log-likelihood of a model in which λ – a measure of phylogenetic signal – was calculated for the data, and then repeated the process when forcing λ to equal 0 (Freckleton et al. 2002). Twice the difference in log-likelihoods of these nested models is distributed as a chi-square statistic, with one degree of freedom. We report effects as slopes of the relationship between body mass and digesta particle size (b_{mass}). When investigating the effect of a particular taxonomic group or digestive strategy, we include a second slope estimate (b_{equid}, $b_{hindgut}$ or $b_{ruminant}$) from a multiple regression model that included b_{mass}. The sign of this second slope indicates whether species coded as having state 1 have larger (positive b) or smaller (negative b) digesta particle size than those with state 0, controlling for

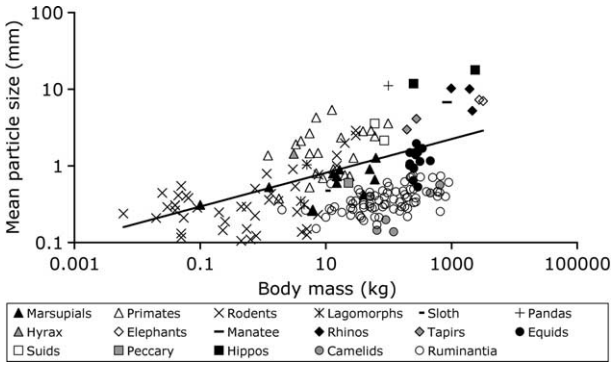

Figure 1. Association between body mass and mean faecal particle size in the mammalian herbivores (one average value per species) investigated in this study. Regression line based phylogenetic generalized least squares (see text).

b_{mass}. All statistical tests reported are two-tailed with significance level (α) of 0.05. We used log-transformed data in all analyses.

Results

Mean faecal particle size (MPS) increased with body mass across species (Fig. 1), and there was no evident discrepancy between species for which several or only one sample had been available (Fig. 2a). In analyses of species averages, the allometric exponent was estimated as 0.15 (95% CI: 0.10 to 0.19) and was significantly different from zero ($t_{191} = 6.02$, $p < 0.001$, $R^2 = 0.16$). In analyses of phylogenetic signal, however, we found strong evidence that more closely related species exhibit more similar trait values ($\lambda = 0.97$ in a correlated model). The log likelihood in this model was -146.6, which was significantly different from $\lambda = 0$, where the log-likelihood was -410.4 (likelihood ratio test, $p < 0.0001$). Although very close to $\lambda = 1$ (likelihood $= -170.2$), the maximum likelihood estimate of 0.97 was also significantly different from $\lambda = 1$ ($p < 0.001$). Thus, we also investigated the scaling of faecal particle size using a regression model in PGLS with the maximum likelihood estimate of λ. This produced a steeper allometric exponent of 0.22 (95% CI: 0.16 to 0.28), which was significantly different from zero (intercept $= -0.31$, $t_{191} = 7.01$, $p < 0.001$). This bivariate model explained 20% of the variation in ingesta particle size ($R^2 = 0.20$). Examining ruminants alone, a regression model in PGLS produced a lower allometric exponent of 0.15 (95% CI: 0.08 to 0.22, intercept $= -0.78$, $t_{80} = 4.46$, $p < 0.0001$; $R^2 = 0.20$).

We also investigated three a priori predictions that were nested phylogenetically, as described above. First, among hindgut fermenters, we found that equids produce smaller ingesta particles for their body mass than other hindgut fermenters ($b_{mass} = 0.25$, $t_{91} = 6.39$, $p < 0.0001$, $b_{equid} = -0.52$, $t_{91} = -2.27$, $p = 0.025$, $R^2 = 0.33$, in a statistical model with equids coded as state 1; Fig. 1b). Second, among the non-ruminants, we found no significant difference between foregut and hindgut fermenters ($b_{mass} = 0.26$, $t_{108} = 6.61$, $p < 0.0001$; $b_{hindgut} = -0.05$,

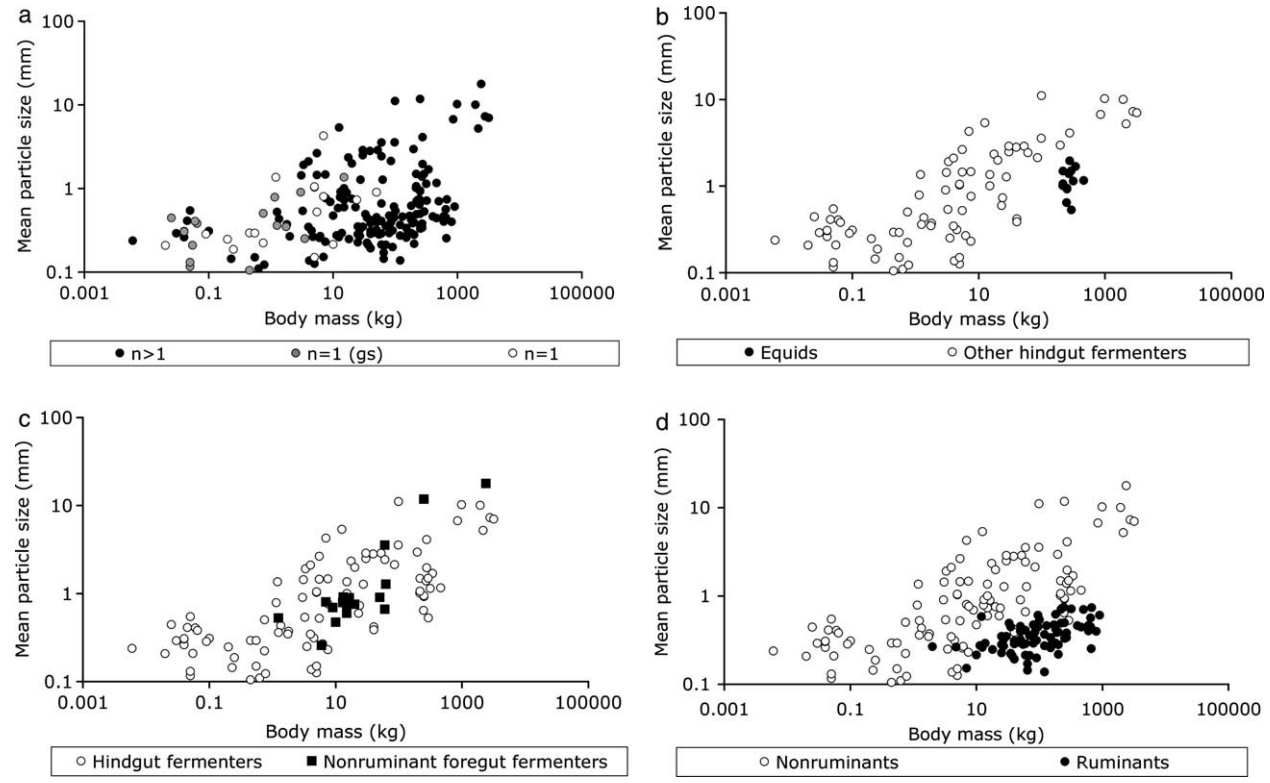

Figure 2. Correlation of body mass and mean faecal particle size in (a) mammalian herbivores, ordered according to the number of samples available per species (gs = group sample); (b) equids (in black) and non-equid hindgut fermenters; (c) non-ruminant foregut fermenters (in black) and hindgut fermenters; (d) functional ruminants (in black) and non-ruminants.

$t_{108} = -0.39$, $p = 0.70$, $R^2 = 0.29$, in a statistical model with hindgut fermenters coded as state 1; Fig. 1c). Lastly, we found that ingesta particle size is significantly smaller in ruminants than in non-ruminants ($b_{mass} = 0.22$, $t_{190} = 7.74$, $p < 0.0001$; $b_{ruminant} = -0.88$, $t_{190} = -4.85$, $p < 0.0001$, $R^2 = 0.30$, in a statistical model with ruminants coded as state 1; Fig. 1d).

Additionally, we used the coefficient from the model that included the ruminants to express faecal MPS as a relative measure. At 4.05 mm/kg$^{0.22}$, the giant panda had the highest relative MPS in the whole dataset. Among the large mammals, relative MPS decreased from the hippos (3.22–3.50 mm/kg$^{0.22}$) to the rhinos (0.97–2.25 mm/kg$^{0.22}$), elephants (1.19–1.27 mm/kg$^{0.22}$), tapirs (0.93–1.19 mm/kg$^{0.22}$), equids (0.15–0.57 mm/kg$^{0.22}$) and ruminants and camelids (0.05–0.34 mm/kg$^{0.22}$). Rodents had values of 0.09–1.37 mm/kg$^{0.22}$; notably, the capybara, at 0.17 mm/kg$^{0.22}$, resembled ruminants of similar body size. At 0.33–3.08 mm/kg$^{0.22}$, primates showed a very large MPS range in this dataset, often surpassing values achieved by equids.

Discussion

Ingesta particle size is one of the most important factors influencing digestive efficiency, but few studies have investigated the degree to which different species can break down food in broad phylogenetic perspective. Our study is the largest analysis of faecal particle size so far conducted and is the first study to use phylogeny-based methods to investigate factors that influence ingesta particle size. We found evidence for negative allometry, with faecal particle size increasing relative to body mass with an exponent of 0.22. We also found support for two of our predictions involving deviations from this allometric relationship. Specifically, particle size was significantly reduced in ruminants (compared to non-ruminants) and equids (compared to other hindgut fermenters). In contrast, we found no significant difference between foregut and hindgut non-ruminant fermenters.

Our study reveals the importance of controlling for phylogeny. In the non-phylogenetic tests, the allometric exponent was estimated as 0.15, whereas it was 0.22 after controlling for phylogeny. This probably reflects that ruminants, which tend to be larger in body size than many other species and also have smaller ingesta particle sizes, represent the most speciose group in this dataset. This will tend to depress the slope of the association when measured across species without controlling for phylogeny. Coupled with the evidence for strong phylogenetic signal, we suggest that the allometric exponent from the phylogeny-based tests should be preferred to the non-phylogenetic tests. However, even when applying phylogeny-based statistics, we should not consider the resulting allometry as a fixed natural law, but as a snapshot of evolutionary time. Consider, for example, how the sequence of decreasing relative faecal particle size (rhino–elephant–equid–ruminant) somewhat resembles the sequence of the peak radiations of the respective groups (Coppens et al. 1978, MacFadden 1992, Cerdeno 1998, Gentry 2000), leading to the hypothesis that a higher chewing efficiency is a characteristic of more recently radiated herbivore groups; in other words, these data could suggest that large mammalian herbivore evolution is characterized by a trend toward increasing chewing efficiency.

Several limitations of the current study are worth mentioning. For a comparative study that comprises a large variety of species such as the present one, it is not feasible to use one common diet because there is no universal food that will be accepted in a similar manner by all species; additionally, species show clear dental adaptations to different diets (Fortelius 1985, Archer and Sanson 2002). Therefore, ideally, a study like the present one should be performed on faeces from free-ranging animals feeding on their natural diets – a task of enormous logistical challenge. Zoo diets usually consist of varying proportions of a forage material (dried – as hay, or fresh – grass, lucerne, browse, green vegetables), pelleted feeds, and various items such as fruits, bread, grain products. Within a species, faecal particle size will increase with an increasing proportion of forage in the ingested diet (Clauss unpubl., in black rhinoceros). The recording of the different proportions of feeds ingested, which necessitates intake trials of at least three consecutive days per animal, was beyond the scope of this study. As differences in faecal particle size between captive and free-ranging animals of the same species have been demonstrated for browsing as opposed to grazing species (Hummel et al. 2008), conclusions derived from the present dataset must be considered with caution, especially when comparing individual species. Similarly, discrepancies in the body masses of the actual animals and the mass estimates used here could make comparisons between species of similar body mass imprecise. Finally, for some species, only one group sample or material from only one individual was available, which should caution against conclusions focussing on these particular species. We see no reason, however, why these values would bias results of broad scale comparisons using our larger dataset.

The results of this study confirm that particle size increases with body mass. Using data from Udén (1978), Pérez-Barberìa and Gordon (1998a) found that faecal particle size scaled to $BM^{0.19}$ in a set of domestic ruminants, rabbits and equids. These authors modelled the scaling of chewing efficiency based on several factors. They suggested that chewing efficiency should, on the one hand, scale to tooth morphology, and, on the other hand, to chewing frequency. Among mammals, teeth scale isometrically, i.e. tooth volume scales to $BM^{1.00}$, and tooth surface area – the effective part of the tooth – to $BM^{0.67}$ (Fortelius 1985, Shipley et al. 1994). The number of chews per gram food ingested scales to $BM^{-0.85}$ (Shipley et al. 1994). Thus, the authors predicted that chewing efficiency scales to $BM^{0.67-0.85} = BM^{-0.18}$, or, inversely, that faecal particle size should scale to $BM^{0.18}$. This exponent lies within the 95% confidence interval determined in our dataset. In contrast, an allometric exponent of 0.33 would have been suspected if it were assumed that particle size, which represents a one-dimensional measure (in mm), should follow the isometric tooth scaling mentioned above (volume $\sim BM^{1.00}$, area $\sim BM^{0.67}$, distance $\sim BM^{0.33}$). However, this exponent was excluded from the 95% confidence interval. Thus, the results could be interpreted to indicate that the whole dental (chewing) surface area and the

chewing frequency are important determinants of ingesta particle size, rather than a linear distance between, for example, enamel ridges.

After accounting for body mass, the remaining large variation in faecal particle size can be explained by differences in dental design and chewing physiology. The herbivorous mammal with probably the least sophisticated dental and masticatory adaptations to its diet is the giant panda (Sanson 2006), which also had the largest faecal particles in this dataset. Hippos, with interlocking canines that prevent a grinding side-stroke, also had particularly large faecal particles. Equids, who display the most complicated molar design in the collection of ungulate molars presented by Jernvall et al. (1996), had significantly finer particles than the other hindgut fermenters of comparable size in our dataset (Fig. 1b). These examples illustrate how dental design can shift a species away from expectations based on body mass alone. It could be expected that detailed analyses based on morphological (dental design) or ecological (feeding type) correlates, for example within the rodents or the primates, could also lead to more insight into additional factors determining chewing efficiency.

The ruminants deserve special attention in this regard. Functional ruminants (true ruminants and camelids) produce finer faecal particles than other mammals (Udén and Van Soest 1982, Freudenberger 1992, Campos-Arceiz et al. 2004; Fig. 1d). This is notably not an effect of having a forestomach per se, as non-ruminant foregut fermenters do not achieve finer faecal particles than hindgut fermenters (Fig. 1c). However, in contrast to what one might expect, rumination is not about chewing food for a longer time; rumination is about sorting (Schwarm et al. 2009). Like many processes in digestive physiology, such as the fermentation of plant material (Hummel et al. 2006), particle size reduction during mastication follows a probability distribution of decreasing returns-the first chew on a new digesta bolus will result in a high degree of particle size reduction, but subsequent chews will be increasingly less effective at reducing particle sizes (Sheine and Kay 1982, Lucas 1994). After a certain number of chews, the probability that food particles that are already sufficiently small will be caught between the chewing blades will be higher than that of catching larger particles, but the small particles are unlikely to be further reduced in their size. Actually, it has been suspected that for any given dentition, a characteristic particle size threshold exists below which particles are very unlikely to be reduced further (Sheine and Kay 1982). In addition, with a higher proportion of already small particles, the probability of fine particles clogging the space between the cutting blades will also increase, thus making further chewing even less efficient. Therefore, after a certain number of chews, swallowing the bolus will be more efficient than continuing to chew; this process intrinsically constrains the advantage that could be gained from increasing chewing time per unit of ingested food.

The only mechanism that would significantly increase the efficiency of chewing in this respect would be a separation of fine particles (that need no longer be chewed) from the larger particles (that should ideally be chewed further). Such a separation is not possible within the oral cavity; no 'sieving' mechanism prior to swallowing is known in mammals. Only functional ruminants achieve such a separation-not in the oral cavity, but in their elaborate forestomachs. Prolonged chewing of the digesta is cost-effective in ruminants, because the ruminant forestomach removes the fine particles from the material that is submitted to repeated mastication (Lechner-Doll et al. 1991). This sorting mechanism is reflected in the fact that the contents of the first sections of the forestomachs of ruminants and camelids comprise not only small particles but also contain larger particles than are found in the distal digestive tract; beyond this point, digesta particle size remains constant and is almost identical to faecal particle size (Udén and Van Soest 1982, Lechner-Doll and von Engelhardt 1989). The sorting mechanisms in ruminants lessens the allometric effect of body size on chewing efficiency, leading to a lower allometric scaling of faecal particle size with body size, thus reducing a potential disadvantage of large size to which other herbivore groups are subjected. It is tempting to speculate that this additional property of the forestomach of functional ruminants was a major factor in the success of this group, particularly the true ruminants, as we know them today.

Prinz and Lucas (1997) identified another problem that occurs if one chews too much on the same bolus: the bolus will disintegrate, and hence its travel across the epiglottis will be dangerous because the increase in saliva, and the constant reduction of the large particle fraction, will reach a point where cohesive forces are too low. Actually, in order to safely swallow a bolus, a certain proportion of large particles is needed. In functional ruminants, the large 'accompanying' particles will be comminuted later, when more recently ingested large particles will take over the 'accompanying' function. To date, in large mammalian herbivores, rumination appears to be the most successful strategy to achieve a high degree of particle size reduction in the digestive tract.

Because of the perceived relevance of digesta retention time, numerous studies have investigated this parameter, often in conjunction with digestibility measurements (reviewed by Clauss et al. 2007). In contrast, measures of chewing efficiency, such as faecal particle size, are rarely included in digestion studies (for exceptions see Gross et al. 1995, Pérez-Barberìa and Gordon 1998b, Clauss et al. 2004, Pérez-Barberìa et al. 2008, Schwarm et al. 2009). A simultaneous evaluation of food intake, ingesta retention time, digestibility, and chewing efficiency will be key for understanding evolutionary variation in digestive physiology. In theory, ingesta retention time should increase with $BM^{0.25}$ (Introduction). The fact that faecal particle size increased with $BM^{0.22}$ in this study could indicate that both allometric effects – that of digesta retention time, and that of digesta particle size – could more or less compensate for each other. This could explain why it has been difficult, so far, to demonstrate an increase in digestive efficiency with increasing body mass across species (Pérez-Barberìa et al. 2004, Clauss and Hummel 2005) or within species (Gross et al. 1996, Pérez-Barberìa et al. 2008). Actually, the concept that increased digesta retention can compensate for a lack of ingestive particle size reduction has been proposed for the comparison of reptilian and mammalian herbivores (Karasov et al. 1986), and potentially long digesta retention times have been evoked as a compensatory mechanism in

gigantic herbivorous dinosaurs that lacked mechanisms of particle size reduction (Farlow 1987, Franz et al. 2009). It is only with the inclusion of faecal particle size measurements that the associations of these different digestive determinants will be disentangled.

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References

Archer, D. and Sanson, G. 2002. Form and function of the selenodont molar in southern African ruminants in relation to their feeding habits. – J. Zool. Lond. 257: 13–26.

Bininda-Emonds, O. R. P. et al. 2007. The delayed rise of present-day mammals. – Nature 446: 507–512.

Campos-Arceiz, A. et al. 2004. Food overlap between Mongolian gazelles and livestock in Omnogobi southern Mongolia. – Ecol. Res. 19: 455–460.

Cerdeno, E. 1998. Diversity and evolutionary trends of the family rhinocerotidae. – Palaeogeogr. Palaeoclimatol. Palaeoecol. 141: 13–34.

Clauss, M. and Hummel, J. 2005. The digestive performance of mammalian herbivores: why big may not be that much better. – Mammal Rev. 35: 174–187.

Clauss, M. et al. 2002. Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer-dichotomy from the other end. – Oecologia 131: 343–349.

Clauss, M. et al. 2004. Intake, ingesta retention, particle size distribution and digestibility in the *hippopotamidae*. – Comp. Biochem. Physiol. A 139: 449–459.

Clauss, M. et al. 2005. Studies on digestive physiology and feed digestibilities in captive Indian rhinoceros (*Rhinoceros unicornis*). – J. Anim. Physiol. Anim. Nutr. 89: 229–237.

Clauss, M. et al. 2007. A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. – Comp. Biochem. Physiol. A 148: 249–265.

Coppens, Y. et al. 1978. Proboscidea. – In: Maglio, V. J. and Cooke, H. B. S. (eds), Evolution of African mammals. Cambridge Univ. Press, pp. 336–367.

Demment, M. W. and Van Soest, P. J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. – Am. Nat. 125: 641–672.

Evans, A. R. et al. 2007. High-level similarity of dentitions in carnivorans and rodents. – Nature 445: 78–81.

Farlow, J. O. 1987. Speculations about the diet and digestive physiology of herbivorous dinosaurs. – Paleobiology 13: 60–72.

Foley, W. J. et al. 1995. The passage of digesta, particle size, and in vitro fermentation rate in the three-toed sloth (*Bradypus tridactylus*). – J. Zool. Lond. 236: 681–696.

Fortelius, M. 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. – Acta Zool. Fenn. 180: 1–76.

Franz, R. et al. 2009. Allometry of visceral organs in living amniotes and its implications for sauropod dinosaurs. – Proc. R. Soc. Lond. B 276: 1731–1736.

Freckleton, R. P. et al. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. – Am. Nat. 160: 712–726.

Freudenberger, D. O. 1992. Gut capacity, frunctional allocation of gut volume and size distributions of digesta particles in two macropodid marsupials (*Macropus robustus robustus* and *M. r. erubescens*) and the feral goat (*Capra hircus*). – Austr. J. Zool. 40: 551–561.

Garland, T. and Ives, A. R. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. – Am. Nat. 155: 346–364.

Gentry, A. W. 2000. The ruminant radiation. – In: Vrba, E. S. and Schaller, G. B. (eds), Antelopes, deer, and relatives. Fossil record, behavioural ecology, systematics, and conservation. Yale Univ. Press, pp. 11–25.

Gross, J. E. et al. 1996. Nutritional ecology of dimorphic herbivores: digeston and passage rates in Nubian ibex. – Oecologia 107: 170–178.

Gross, J. E. et al. 1995. Feeding and chewing behaviors of Nubian ibex: compensation for sex-related differences in body size. – Funct. Ecol. 9: 385–393.

Hume, I. D. 1999. Marsupial nutrition. – Cambridge Univ. Press.

Hummel, J. et al. 2006. Forage fermentation patterns and their implications for herbivore ingesta retention times. – Funct. Ecol. 20: 989–1002.

Hummel, J. et al. 2008. Differences in fecal particle size between free-ranging
and captive individuals of two browser species. – Zoo Biol. 27: 70–77.

Illius, A. W. and Gordon, I. J. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. – Oecologia 89: 428–434.

Janis, C. 1976. The evolutionary strategy of the equidae and the origins of rumen and caecal digestion. – Evolution 30: 757–774.

Jernvall, J. et al. 1996. Molar tooth diversity, disparity, and ecology in Cenozoic ungulate radiations. – Science 274: 1489–1492.

Karasov, W. H. et al. 1986. How do food passage rate and assimilation differ between herbivorous lizards and nonruminants mammals? – J. Comp. Physiol. B 156: 599–609.

Langer, P. 1988. The mammalian herbivore stomach. – Gustav Fischer.

Lechner-Doll, M. et al. 1991. Factors affecting the mean retention time of particles in the forestomach of ruminants and camelids. – In: Tsuda, T. et al. (eds.), Physiological aspects of digestion and metabolism in ruminants. Academic Press, pp. 455–482.

Lechner-Doll, M. and von Engelhardt, W. 1989. Particle size and passage from the forestomach in camels compared to cattle and sheep fed a similar diet. – J. Anim. Physiol. Anim. Nutr. 61: 120–128.

Logan, M. 2003. Effect of tooth wear on the rumination-like behavior, or merycism, of free-ranging koalas (*Phascolarctos cinereus*). – J. Mammal. 84: 897–902.

Lord, R. D. 1994. A descriptive account of capybara behavior. – Stud. Neotrop. Fauna Environ. 29: 11–22.

Lucas, P. W. 1994. Categorisation of food items relevant to oral processing. – In: Chivers, D. J. and Langer, P. (eds), The digestive system in mammals - food, form and function. Cambridge Univ. Press, pp. 197–218.

MacFadden, B. J. 1992. Fossil horses. – Cambridge Univ. Press.

Martins, E. P. and Hansen, T. F. 1997. Phylogenies and the comparative method: a general approach to incorporating

phylogenetic information into analysis of interspecific data. – Am. Nat. 149: 646–667.
McLeod, M. N. and Minson, D. J. 1988a. Breakdown of large particles in forage by simulated digestion and detrition. – J. Anim. Sci. 66: 1000–1004.
McLeod, M. N. and Minson, D. J. 1988b. Large particle breakdown by cattle eating ryegrass and alfalfa. – J. Anim. Sci. 66: 992–999.
Moir, R. J. 1965. The comparative physiology of ruminant-like animals. – In: Physiology of digestion in the ruminant. Butterworth, pp. 1–14.
Murphy, M. R. and Nicoletti, J. M. 1984. Potential reduction of forage and rumen digesta particle size by microbial action. – J. Dairy Sci. 67: 1221–1226.
Pagel, M. and Meade, A. 2007. BayesTraits, ver.1.0. – <www.evolution.rdg.ac.uk>.
Parra, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. – In: Montgomery, G. G. (ed.), The ecology of arboreal folivores. Smithsonian Inst. Press, pp. 205–229.
Pérez-Barberìa, F. J. et al. 2004. The evolution of phylogenetic differences in the efficiency of digestion in ruminants. – Proc. R. Soc. Lond. B 271: 1081–1090.
Pérez-Barberìa, F. J. and Gordon, I. J. 1998a. Factors affecting food comminution during chewing in ruminants: a review. – Biol. J. Linn. Soc. 63: 233–256.
Pérez-Barberìa, F. J. and Gordon, I. J. 1998b. The influence of molar occlusal surface area on the voluntary intake, digestion, chewing behaviour and diet selection of red deer. – J. Zool. Lond. 245: 307–316.
Pérez-Barberìa, F. J. et al. 2008. Does the Jarman-Bell principle at intra-specific level explain sexual segregation in polygonous ungulates? Sex differences in forage digestibility in Soay sheep. – Oecologia 157: 21–30.
Poppi, D. P. et al. 1980. The validity of the critical size theory for particles leaving the rumen. – J. Agric. Sci. Cambr. 94: 275–280.
Prinz, J. F. and Lucas, P. W. 1997. An optimization model for mastication and swallowing in mammals. – Proc. R. Soc. Lond. B 264: 1715–1721.
Reilly, S. M. et al. 2001. Prey processing in amniotes: biomechanical and behavioral patterns of food reduction. – Comp. Biochem. Physiol. A 128: 397–415.
Rensberger, J. M. 1973. An occlusal model for mastication and dental wear in herbivorous mammals. – J. Paleontol. 47: 515–528.
Sanson, G. D. 2006. The biomechanics of browsing and grazing. – Am. J. Bot. 93: 1531–1545.
Schwarm, A. et al. 2009. More efficient mastication allows increasing intake without compromising digestibility or necessitating a larger gut: comparative feeding trials in banteng (*Bos javanicus*) and pygmy hippopotamus (*Hexaprotodon liberiensis*). – Comp. Biochem. Physiol. A 152: 504–512.
Sheine, W. S. and Kay, R. F. 1982. A model for comparison of masticatory effectiveness in primates. – J. Morphol. 172: 139–149.
Shipley, L. A. et al. 1994. The scaling of intake rate in mammalian herbivores. – Am. Nat. 143: 1055–1082.
Spalinger, D. E. and Robbins, C. T. 1992. The dynamics of particle flow in the rumen of mule deer and elk. – Physiol. Zool. 65: 379–402.
Udén, P. 1978. Comparative studies on rate of passage, particle size, and rate of digestion in ruminants, equines, rabbits, and man. – Cornell Univ.
Udén, P. and Van Soest, P. J. 1982. The determination of digesta particle size in some herbivores. – Anim. Feed Sci. Technol. 7: 35–44.

Appendix 1. Original data from this study. DT = digestion type (H = hindgut fermenter, F = nonruminant foregut fermenter, R = ruminant); n is the number of faecal samples analysed (gs = group sample pooled from a group of animals; BM = body mass (mean if actually measured) in kg, followed by the SD = standard deviation (if body mass was actually measured); MPS = mean particle size in mm, followed by the SD; rMPS = relative mean particle size, expressed in $mm/kg^{0.22}$.

Species			DT	n	BM	SD	MPS	SD	rMPS
Monodelphis domestica	Didelphimorphia	Didelphidae	H	2 (gs)	0.100	–	0.3096	0.2087	0.51
Phascolarctos cinereus	Diprodontia	Phascolarctidae	H	5	6.190	1.128	0.2684	0.0482	0.18
Vombatus ursinus	Diprodontia	Vombatidae	H	3	40.000	–	0.4195	0.0716	0.19
Bettongia penicillata	Diprodontia	Potoridae	F	2 (gs)	1.250	0.354	0.5253	0.5419	0.50
Dendrolagus matschiei	Diprodontia	Macropodidae	F	3	13.000	–	0.7902	0.0884	0.45
Macropus agilis	Diprodontia	Macropodidae	F	2	15.000	–	0.7302	0.0285	0.40
Macropus fuliginosus	Diprodontia	Macropodidae	F	1	50.000	–	0.9027	–	0.38
Macropus giganteus	Diprodontia	Macropodidae	F	3	60.000	25.000	0.6619	0.4235	0.27
Macropus parma	Diprodontia	Macropodidae	F	2 (gs)	6.000	–	0.257	0.1152	0.17
Macropus rufogriseus	Diprodontia	Macropodidae	F	3	16.500	0.866	0.8935	0.0916	0.48
Macropus rufus	Diprodontia	Macropodidae	F	2	62.500	–	1.2745	0.3221	0.51
Wallabia bicolor	Diprodontia	Macropodidae	F	2	15.000	–	0.5967	0.1061	0.33
Hapalemur griseus	Primates	Lemuridae	H	1	1.200	–	1.3616	–	1.31
Lemur catta	Primates	Lemuridae	H	3	3.330	0.289	1.9137	0.6248	1.47
Varecia variegata	Primates	Lemuridae	H	4	4.000	–	2.1139	0.8335	1.56
Alouatta palliata	Primates	Cebidae	H	1	7.000	–	4.2799	–	2.79
Lagothrix lagotricha	Primates	Cebidae	H	2	7.500	4.243	1.4689	0.5602	0.94
Pithecia pithecia	Primates	Cebidae	H	2	1.800	0.283	0.3734	0.0283	0.33
Cercopithecus pygerythrus	Primates	Cercopithecidae	H	1	5.500	–	0.5246	–	0.36
Macaca sylvanus	Primates	Cercopithecidae	H	1	24.000	–	0.7321	–	0.36
Mandrillus sphinx	Primates	Cercopithecidae	H	2	27.500	0.707	1.2757	0.4009	0.62
Presbytis obscurus	Primates	Cercopithecidae	F	1	7.000	–	0.8022	–	0.52
Presbytis entellus	Primates	Cercopithecidae	F	2 (gs)	20.000	1.414	0.7557	0.0244	0.39
Presbytis cristata	Primates	Cercopithecidae	F	3 (gs)	13.170	2.021	0.9121	0.1149	0.52
Pygathrix nemaeus	Primates	Cercopithecidae	F	5	9.000	1.414	0.692	0.2713	0.43
Theropithecus gelada	Primates	Cercopithecidae	H	6	17.500	–	2.3431	0.9424	1.25
Hylobates lar	Primates	Hylobatidae	H	2	5.500	–	2.6485	0.8821	1.82
Hylobates lar moloch	Primates	Hylobatidae	H	2	5.500	0.707	1.4543	0.2147	1.00
Hylobates syndactylus	Primates	Hylobatidae	H	4	12.500	1.683	5.3762	3.8075	3.08
Gorilla gorilla	Primates	Pongidae	H	8	97.560	55.537	3.5757	1.5837	1.31
Pan paniscus	Primates	Pongidae	H	5	39.120	9.366	2.8217	0.5834	1.26
Pan troglodytes	Primates	Pongidae	H	5	52.220	26.187	2.887	1.1119	1.21
Pongo pygmaeus	Primates	Pongidae	H	5	60.000	37.495	2.4292	1.6022	0.99
Choloepus didactylus	Xenarthra	Megalonychidae	F	5	10.000	1.414	0.4726	0.1887	0.28
Lepus europaeus	Lagomorpha	Leporidae	H	5	4.500	–	0.3134	0.0903	0.23
Oryctolagus cuniculus	Lagomorpha	Leporidae	H	5	4.000	–	0.3464	0.0427	0.26
Cynomys ludovicianus	Rodentia	Sciuridae	H	1 (gs)	1.150	–	0.7907	–	0.77
Marmota bobac	Rodentia	Sciuridae	H	1	5.000	–	0.1501	–	0.11
Marmota marmota	Rodentia	Sciuridae	H	1	5.000	–	1.0513	–	0.74
Sciurus carolinensis	Rodentia	Sciuridae	H	1	0.450	–	0.2941	–	0.35
Sciurus variegatoides	Rodentia	Sciuridae	H	1	0.550	–	0.2928	–	0.33
Xerus inauris	Rodentia	Sciuridae	H	1 (gs)	0.750	–	0.5029	–	0.54
Castor canadensis	Rodentia	Castoridae	H	2	30.000	–	2.4945	0.2709	1.18
Castor fiber	Rodentia	Castoridae	H	3	30.000	–	2.887	0.3855	1.37
Pedetes capensis	Rodentia	Pedetidae	H	1 (gs)	3.500	–	0.2508	–	0.19
Jaculus jaculus	Rodentia	Dipodidae	H	1 (gs)	0.055	–	0.2095	–	0.40
Acomys russatus	Rodentia	Muridae	H	2 (gs)	0.045	–	0.4119	0.0702	0.81
Lemniscomys barbarus	Rodentia	Muridae	H	1 (gs)	0.040	–	0.308	–	0.63
Mastomys natalensis	Rodentia	Muridae	H	1 (gs)	0.065	–	0.382	–	0.70
Micromys minutus	Rodentia	Muridae	H	2 (gs)	0.006	–	0.238	0.0416	0.73
Mus musculus	Rodentia	Muridae	H	1	0.020	–	0.2085	–	0.49
Cricetomys emini	Rodentia	Cricetidae	H	1 (gs)	1.250	–	0.3611	–	0.34
Cricetulus griseus	Rodentia	Cricetidae	H	1 (gs)	0.040	–	0.3046	–	0.62
Gerbillus perpallidus	Rodentia	Cricetidae	H	2 (gs)	0.040	–	0.2615	0.0169	0.53
Graphiurus murinus	Rodentia	Cricetidae	H	1 (gs)	0.025	–	0.4441	–	1.00
Hypogeomys antimena	Rodentia	Cricetidae	H	2	1.350	–	0.4323	0.1427	0.40
Microtus brandti	Rodentia	Cricetidae	H	1 (gs)	0.050	–	0.1164	–	0.22
Microtus fortis	Rodentia	Cricetidae	H	1 (gs)	0.050	–	0.131	–	0.25
Phodopus roborovskii	Rodentia	Cricetidae	H	2 (gs)	0.030	–	0.2911	0.0586	0.63
Phodopus sungorus	Rodentia	Cricetidae	H	3 (gs)	0.040	–	0.3074	0.0034	0.62
Seketamys calurus	Rodentia	Cricetidae	H	1 (gs)	0.060	–	0.4073	–	0.76
Ctenodactylus gundi	Rodentia	Ctenodactylidae	H	1	0.250	–	0.1871	–	0.25
Atherurus africanus	Rodentia	Hystricidae	H	1 (gs)	1.750	–	0.3483	–	0.31
Hystrix africaeaustralis	Rodentia	Hystricidae	H	1 (gs)	15.000	–	1.3612	–	0.75
Hystrix cristata	Rodentia	Hystricidae	H	5 (gs)	20.000	–	1.9895	0.9872	1.03
Hystrix indica	Rodentia	Hystricidae	H	2 (gs)	15.000	–	1.005	0.0754	0.55
Petromus typicus	Rodentia	Petromuridae	H	1	0.200	–	0.2471	–	0.35
Heterocephalus glaber	Rodentia	Bathyergidae	H	2 (gs)	0.050	–	0.5468	0.1048	1.06
Chinchilla chinchilla	Rodentia	Chinchillidae	H	3 (gs)	0.550	0.050	0.1502	0.0547	0.17

Species			DT	n	BM	SD	MPS	SD	rMPS
Lagostomus maximus	Rodentia	Chinchillidae	H	5	4.130	0.790	0.1375	0.0114	0.10
Cavia aperea	Rodentia	Caviidae	H	3 (gs)	0.630	–	0.1099	0.0215	0.12
Cavia aperea f. porcellus	Rodentia	Caviidae	H	6 (gs)	0.780	0.075	0.1228	0.0102	0.13
Dolichotis patagonum	Rodentia	Caviidae	H	5 (gs)	7.500	0.354	0.2308	0.0464	0.15
Galea musteloides	Rodentia	Caviidae	H	1 (gs)	0.450	–	0.1051	–	0.13
Kerodon rupestris	Rodentia	Caviidae	H	1	0.750	–	0.2233	–	0.24
Hydrochaerus hydrochaeris	Rodentia	Hydrochaeridae	H	3	40.000	–	0.3868	0.0578	0.17
Dasyprocta azarae	Rodentia	Dasyproctidae	H	1 (gs)	3.000	–	0.9024	–	0.71
Dasyprocta leporina	Rodentia	Dasyproctidae	H	2 (gs)	3.250	–	0.5393	0.3939	0.42
Octodon degus	Rodentia	Octodontidae	H	2 (gs)	0.230	–	0.1441	0.0164	0.20
Spalacopus cyanus	Rodentia	Octodontidae	H	1	0.090	–	0.2852	–	0.48
Capromys pilorides	Rodentia	Capromyidae	H	3	5.000	0.500	0.126	0.0297	0.09
Myocastor coypus	Rodentia	Myocastoridae	H	5 (gs)	7.600	0.894	0.765	0.3442	0.49
Procavia capensis	Hyracoidea	Procaviidae	H	2 (gs)	3.080	0.106	1.4364	1.0848	1.12
Elephas maximus	Proboscidea	Elephantidae	H	18	3183.670	821.540	7.0195	3.7525	1.19
Loxodonta africana	Proboscidea	Elephantidae	H	13	2764.620	1014.656	7.2848	2.9278	1.27
Trichechus manatus	Sirenia	Trichechidae	H	4	850.000	57.735	6.7287	3.8258	1.53
Equus africanus f. asinus	Perissodactyla	Equidae	H	11	216.360	113.227	1.0646	0.5555	0.33
Equus africanus somalicus	Perissodactyla	Equidae	H	4	268.750	23.936	1.3898	0.4776	0.41
Equus grevyi	Perissodactyla	Equidae	H	5	342.000	10.955	1.6918	0.9495	0.47
Equus hemionus kiang	Perissodactyla	Equidae	H	6	245.000	5.477	0.6449	0.1583	0.19
Equus hemionus kulan	Perissodactyla	Equidae	H	5	250.000	–	0.9464	0.3523	0.28
Equus hemionus onager	Perissodactyla	Equidae	H	2	250.000	–	0.9268	0.0483	0.28
Equus przewalskii	Perissodactyla	Equidae	H	5	292.000	40.866	0.5305	0.0814	0.15
Equus przewalskii f. caballus	Perissodactyla	Equidae	H	37	460.000	223.709	1.1642	0.5327	0.30
Equus quagga antiquorum	Perissodactyla	Equidae	H	3	216.670	28.868	1.4914	0.7224	0.46
Equus quagga boehmi	Perissodactyla	Equidae	H	6	275.000	27.386	1.9624	0.8105	0.57
Equus quagga burchelli	Perissodactyla	Equidae	H	2	215.000	21.213	1.0146	0.0114	0.31
Equus quagga chapmani	Perissodactyla	Equidae	H	5	290.000	22.361	1.4985	1.2459	0.43
Equus zebra hartmannae	Perissodactyla	Equidae	H	5	314.000	21.909	1.1418	0.4181	0.32
Ceratotherium simum	Perissodactyla	Rhinocerotidae	H	8	1938.750	370.769	10.0477	2.8326	1.90
Diceros bicornis	Perissodactyla	Rhinocerotidae	H	12	985.000	200.839	10.2459	4.9816	2.25
Rhinoceros unicornis	Perissodactyla	Rhinocerotidae	H	6	2150.000	151.658	5.227	2.3469	0.97
Tapirus indicus	Perissodactyla	Tapiridae	H	5	275.000	17.678	4.1099	1.934	1.19
Tapirus terrestris	Perissodactyla	Tapiridae	H	10	195.500	17.552	2.968	1.3287	0.93
Ailuropoda melanoleuca	Carnivora	Ailuridae	H	8	98.750	9.910	11.115	8.9169	4.05
Ailurus fulgens	Carnivora	Ailuridae	H	5 (gs)	5.000	–	1.0317	0.4037	0.72
Babyrousa babyrussa	Cetartiodactyla	Suidae	F	3	60.000	–	3.555	1.5333	1.44
Phacochoerus aethiopicus	Cetartiodactyla	Suidae	H	5	85.000	–	2.1359	0.228	0.80
Tayassu tajacu	Cetartiodactyla	Tayassuidae	H	5	23.000	–	0.5969	0.1019	0.30
Choeropsis liberiensis	Cetartiodactyla	Hippopotamidae	F	9	250.000	–	11.788	3.0969	3.50
Hippopotamus amphibius	Cetartiodactyla	Hippopotamidae	F	6	2391.600	263.686	17.807	8.892	3.22
Camelus dromedarius	Cetartiodactyla	Camelidae	R	5	460.000	22.361	0.4436	0.1036	0.12
Camelus ferus	Cetartiodactyla	Camelidae	R	5	650.000	–	0.5656	0.1337	0.14
Lama guanicoe	Cetartiodactyla	Camelidae	R	5	90.000	–	0.199	0.0842	0.07
Lama guanicoe f. glaman	Cetartiodactyla	Camelidae	R	5	120.000	–	0.1378	0.0431	0.05
Lama guanicoe f. pacos	Cetartiodactyla	Camelidae	R	5 (gs)	65.000	–	0.1441	0.0557	0.06
Lama vicugna	Cetartiodactyla	Camelidae	R	5	51.000	2.236	0.3996	0.5334	0.17
Tragulus javanicus	Cetartiodactyla	Tragulidae	R	5 (gs)	2.000	–	0.2681	0.0693	0.23
Antilocapra americana	Cetartiodactyla	Antilocapridae	R	3	40.000	–	0.2866	0.0092	0.13
Giraffa camelopardalis	Cetartiodactyla	Giraffidae	R	14	672.140	327.459	0.7398	0.3228	0.18
Okapia johnstoni	Cetartiodactyla	Giraffidae	R	9	243.330	32.596	0.7485	0.3613	0.22
Alces alces	Cetartiodactyla	Cervidae	R	3	320.000	–	0.716	0.2035	0.20
Axis axis	Cetartiodactyla	Cervidae	R	3	85.000	–	0.3924	0.1853	0.15
Blastocerus dichotomus	Cetartiodactyla	Cervidae	R	2	80.000	–	0.4733	0.1138	0.18
Capreolus capreolus	Cetartiodactyla	Cervidae	R	3	25.000	–	0.2265	0.0311	0.11
Cervus albirostris	Cetartiodactyla	Cervidae	R	7	130.000	–	0.4613	0.178	0.16
Cervus elaphus	Cetartiodactyla	Cervidae	R	3	170.000	–	0.4713	0.1264	0.15
Cervus eldi	Cetartiodactyla	Cervidae	R	3	120.000	–	0.3671	0.2418	0.13
Cervus nippon	Cetartiodactyla	Cervidae	R	3	70.000	–	0.3554	0.0678	0.14
Cervus timorensis	Cetartiodactyla	Cervidae	R	3	150.000	–	0.3379	0.1031	0.11
Cervus unicolor	Cetartiodactyla	Cervidae	R	3	200.000	–	0.3904	0.0762	0.12
Dama dama	Cetartiodactyla	Cervidae	R	3	60.000	–	0.2892	0.0425	0.12
Elaphodus cephalophus	Cetartiodactyla	Cervidae	R	3	35.000	–	0.4472	0.1705	0.20
Muntiacus muntjak	Cetartiodactyla	Cervidae	R	4	25.000	–	0.283	0.07	0.14
Muntiacus reevesi	Cetartiodactyla	Cervidae	R	5	11.400	4.219	0.2754	0.1668	0.16
Odocoileus hemionus	Cetartiodactyla	Cervidae	R	3	80.000	–	0.2922	0.1006	0.11
Odocoileus virginianus	Cetartiodactyla	Cervidae	R	3	70.000	–	0.2128	0.0219	0.08
Ozotoceros beoarticus	Cetartiodactyla	Cervidae	R	2	35.000	–	0.4471	0.1717	0.20
Pudu pudu	Cetartiodactyla	Cervidae	R	2	12.000	–	0.5857	0.4249	0.34
Rangifer tarandus	Cetartiodactyla	Cervidae	R	3	180.000	–	0.2936	0.0237	0.09

Appendix 1 (*Continued*)

Species			DT	n	BM	SD	MPS	SD	rMPS
Addax nasomaculatus	Cetartiodactyla	Bovidae	R	3	85.000	–	0.3139	0.1071	0.12
Aepyceros melampus	Cetartiodactyla	Bovidae	R	3	55.000	–	0.2818	0.0181	0.12
Alcelaphus buselaphus	Cetartiodactyla	Bovidae	R	3	180.000	–	0.4226	0.1225	0.13
Antidorcas marsupialis	Cetartiodactyla	Bovidae	R	6	30.000	–	0.3498	0.0935	0.17
Antilope cervicapra	Cetartiodactyla	Bovidae	R	3	33.000	–	0.492	0.0471	0.23
Bison bison	Cetartiodactyla	Bovidae	R	3	650.000	–	0.4499	0.199	0.11
Bison bonasus	Cetartiodactyla	Bovidae	R	3	600.000	–	0.459	0.1574	0.11
Bos frontalis	Cetartiodactyla	Bovidae	R	3	800.000	–	0.3989	0.1299	0.09
Bos grunniens	Cetartiodactyla	Bovidae	R	3	400.000	–	0.4623	0.0872	0.12
Bos javanicus	Cetartiodactyla	Bovidae	R	3	600.000	–	0.4023	0.0932	0.10
Bos primigenius f. taurus	Cetartiodactyla	Bovidae	R	6	661.670	510.624	0.2539	0.0644	0.06
Boselaphus tragocamelus	Cetartiodactyla	Bovidae	R	4	220.000	–	0.7075	0.2317	0.22
Bubalus arnee	Cetartiodactyla	Bovidae	R	3	900.000	–	0.6085	0.1229	0.14
Bubalus depressicornis	Cetartiodactyla	Bovidae	R	2	150.000	–	0.2581	0.0008	0.09
Budorcas taxicolor	Cetartiodactyla	Bovidae	R	3	270.000	–	0.339	0.1799	0.10
Capra falconeri	Cetartiodactyla	Bovidae	R	3	50.000	–	0.3216	0.0407	0.14
Capra hircus	Cetartiodactyla	Bovidae	R	3	40.000	–	0.1929	0.0455	0.09
Capra ibex	Cetartiodactyla	Bovidae	R	3	60.000	–	0.409	0.035	0.17
Cephalophus monticola	Cetartiodactyla	Bovidae	R	3	7.000	–	0.1521	0.0245	0.10
Cephalophus natalensis	Cetartiodactyla	Bovidae	R	5 (gs)	12.400	0.894	0.2617	0.0219	0.15
Cervus duvauceli	Cetartiodactyla	Bovidae	R	4	200.000	–	0.2185	0.0552	0.07
Connochaetes gnou	Cetartiodactyla	Bovidae	R	3	160.000	–	0.2942	0.0536	0.10
Damaliscus pygargus	Cetartiodactyla	Bovidae	R	3	65.000	–	0.1712	0.0259	0.07
Dorcatragus megalotis	Cetartiodactyla	Bovidae	R	1	10.000	–	0.2144	–	0.13
Elaphurus davidianus	Cetartiodactyla	Bovidae	R	3	120.000	–	0.274	0.0898	0.10
Gazella dama	Cetartiodactyla	Bovidae	R	2	50.000	–	0.4539	0.1117	0.19
Gazella dorcas	Cetartiodactyla	Bovidae	R	3	18.000	–	0.2481	0.0048	0.13
Gazella subgutturosa	Cetartiodactyla	Bovidae	R	3	27.000	–	0.2705	0.0195	0.13
Hippotragus equinus	Cetartiodactyla	Bovidae	R	3	270.000	–	0.3811	0.0267	0.11
Hippotragus niger	Cetartiodactyla	Bovidae	R	3	220.000	–	0.4944	0.2089	0.15
Kobus ellipsiprymnus	Cetartiodactyla	Bovidae	R	3	190.000	–	0.3848	0.1166	0.12
Kobus leche	Cetartiodactyla	Bovidae	R	4	90.000	–	0.3145	0.07	0.12
Litocranius walleri	Cetartiodactyla	Bovidae	R	2	37.000	–	0.2104	0.0127	0.10
Madoqua kirki	Cetartiodactyla	Bovidae	R	2	4.750	0.354	0.264	0.0009	0.19
Nemorhaedus goral	Cetartiodactyla	Bovidae	R	3	35.000	–	0.2205	0.0304	0.10
Oreamnos americanus	Cetartiodactyla	Bovidae	R	3	60.000	–	0.2137	0.0943	0.09
Oreotragus oreotragus	Cetartiodactyla	Bovidae	R	4	13.750	0.500	0.2924	0.0608	0.16
Oryx dammah	Cetartiodactyla	Bovidae	R	3	180.000	–	0.6202	0.2916	0.20
Oryx gazella	Cetartiodactyla	Bovidae	R	2	200.000	–	0.2802	0.0022	0.09
Ovibos moschatus	Cetartiodactyla	Bovidae	R	5	252.000	56.303	0.3318	0.1887	0.10
Ovis ammon aries	Cetartiodactyla	Bovidae	R	3	25.000	–	0.3504	0.1027	0.17
Ovis ammon musimon	Cetartiodactyla	Bovidae	R	3	40.000	–	0.3095	0.0501	0.14
Pseudois nayaur	Cetartiodactyla	Bovidae	R	2	27.000	–	0.3217	0.2978	0.16
Redunca redunca	Cetartiodactyla	Bovidae	R	3	50.000	–	0.2945	0.1635	0.12
Rupicapra rupicapra	Cetartiodactyla	Bovidae	R	3	50.000	–	0.4014	0.0844	0.17
Saiga tartarica	Cetartiodactyla	Bovidae	R	3	35.000	–	0.2244	0.0308	0.10
Syncerus caffer	Cetartiodactyla	Bovidae	R	3	600.000	–	0.4652	0.0697	0.11
Tragelaphus angasi	Cetartiodactyla	Bovidae	R	3	100.000	–	0.5392	0.1736	0.20
Tragelaphus eurycerus	Cetartiodactyla	Bovidae	R	3	250.000	–	0.4984	0.0692	0.15
Tragelaphus imberbis	Cetartiodactyla	Bovidae	R	3	95.000	–	0.6063	0.1419	0.22
Tragelaphus oryx	Cetartiodactyla	Bovidae	R	3	500.000	–	0.7036	0.2758	0.18
Tragelaphus spekei	Cetartiodactyla	Bovidae	R	4	95.000	–	0.4471	0.1551	0.16
Tragelaphus strepsiceros	Cetartiodactyla	Bovidae	R	5	230.000	–	0.7294	0.256	0.22